

Hybrid zone and its genetic analysis: implication for conservation

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Abstract: Hybrid zone is a very critical concept within the evolutionary biology, because it would offer us a better insight to understand the evolutionary role of gene flow and hybridization based on the cline model. This minireview presents an expatiation of history perspectives and research developments upon basic concepts including hybrid zones, hybridization, hybrid and its the genetic cline model. Moreover, by figuring out the existing problem around the hybrids within conservative theory and practices, it suggests that the theory of hybrid zone be introduced into conservation biology and it would be provide a broader and more open theoretical background for conservative research and practices.

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Introduction

Hybridization and, in particular, the maintenance of hybrid zones have traditionally received considerable attention because of their important contributions to the understanding of the evolutionary patterns and process. Within hybrid zones, hybridization and introgression can: (1) increase genetic diversity of population/species, (2) cause the transfer of genetic adaptations, (3) induce the breakdown or reinforce reproductive barriers between closely related groups, and (4) lead to the emergence of new ecotypes or species (Petit *et al.* 1999). Hybrid zone has been one of the hotspots in the evolutionary biology for more than one century. However, since 1990, its theory gradually became mature and explosive empirical data derived from multidisciplinary studies of many hybrid zones. Until now, the issues around hybrid zone and hybridization are far from resolved, though hybridization and introgression putatively had been regarded as accepted important sources of new variations.

Hybrid zone and hybridization

The hybrid-zone issue stems on the following simple problems as: are hybrid population important sources of evolutionary novelties? Should hybrid populations be recognized as distinct Operational Taxonomic Units, iike sub-species, species, etc. (Harrison 1993) ?

Although records of crosses between species and varieties have been documented from the sixteenth and seventeenth centuries (Zirkle 1932,1934), the modern literature on hybridization could be traced to the systematic studies of plant hybrids conducted by Kolrcuter and Linnaeus during

the mid-eighteenth century (Stebbins 1959). At that time, a commonly held view concerned the difference between "varieties" and "species" was that crosses between varieties produced mongrel offspring that were perfectly fertile, whereas crosses between species produced sterile hybrid offspring. Therefore from the perspectives of the most naturalists in the nineteenth century, sterility was a criterion for species and hybrid was defined sterile. Even today, this criterion is still supported by certain biologists and explained as that species were specially endowed with sterility in order to prevent their confusion. Darwin (1872) disagreed with this prevailing view and concluded that the sterile rule was not universal, he then pointed out the circularity of argument upon the fertility of crossed between varieties as opposed to the sterility of crossed between species.

From the contrasting view of genetics and plant and animal breeding, hybrid simply refers to the offspring of genetically distinct parents. Such a definition seems appropriate for experimental crosses in which parents are selected for their difference(s) in one or more traits. In most sexually reproducing species, however every individual of the next generation would own a unique genotype and thus be a "hybrid". Defined in this way, the term "hybrid" would not describe a restricted class of individuals. Stebbins (1959) defined hybridization as "the crossing of individuals belonging in separate populations that have different adaptive norms". Presently, an operational definition, which does not require subjective determination of whether populations are "unlike" or "have different adaptive norms", is that the hybridization is "the interbreeding of individuals from two populations, or groups of population, which are distinguishable on the basis of one or more heritable characters" (Woodruff 1973; Harrison 1990). Moreover, this kind of population could be called species based on the phylogenetic species concept (PSC), even only one trait differs between populations (Cracraft 1983,1989; Nixon and Wheeler 1990). One of visible advantages of this definition

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is that consistent application does not depend on agreement on species concept.

Hybrid zones occur when genetically distinct groups of individuals meet and mate, resulting in at least some offspring of mixed ancestry (Harrison 1990; Barton and Hewitt 1989). The definition is intentionally broad and includes situations ranging from sporadic or occasional hybridization between species that are broadly sympatric to narrow zones of hybridization between taxa with effectively parapatric distributions. Some cases result in a "hybrid swarm", a diverse array of recombinant types; whereas only F_1 offspring are found in other situations. This definition does not depend on either knowledge of the history of the interaction or an understanding of the evolutionary forces acting to maintain it, furthermore, it makes no attempt to discriminate on the basis of the geography of hybridization. However, many articles provided a more restrictive definitions, for example, Mayr (1942) regarded hybrid zone as regions of secondary intergradation, and other people thought that hybrid zone was derived from secondary contact between previously isolated populations (Rising 1983; Littlejohn and Watson, 1985). Yet, Barton and Hewitt (1981) suggested that such definition include the dynamics of the hybrid zones.

Examples of natural hybridization are common among plants, and many plants species appear to be interconnected by limited gene exchange (Stebbins 1950; Grant 1981). Stebbins (1959) further suggested that hybridization between distinct forms (species or subspecies) is "the rule of flowering plants" and urged that particular attention be given to examples of sympatric closely related species that do not hybridize. Plant hybrid zones tend to be diffuse (not geographically well defined) and are often characterized by local hybrid swarms.

In animals, diversification over time is portrayed as a series of dichotomous branching events, suggesting that reticulate evolution occurs rarely. Mayr (1963) well expressed the view, as "the evolution importance of hybridization seems small in the better-known groups of animals". Despite the supposed rarity of animal hybrids in nature, hybridization has been a major focus of animal studies in animal evolution (Harrison 1990). Hybrid zone of animals usually appears as abrupt discontinuities between differentiated groups of populations that are themselves relatively homogenous over large areas. These discontinuities still need an explanation. How did they arise? And why do they persist? Are hybrid zones stable or transient? Presumably as a consequence of their different experiences with hybridization in natural populations, botanists and zoologists have developed rather different views of the "evolutionary role" of hybridization. Zoologists have been more reluctant to recognize hybridization as a catalyst of evolutionary change or innovation. In recent years, zoologists have most often treated hybrid zones as "windows on the evolutionary process" (Harrison 1990) or as "natural laboratories" (Hewitt 1988) in which to explore the operation of evolutionary

forces, the nature of barriers to gene exchange, and the genetic differences responsible for these barriers, compared with botanists only viewing hybridization as a creative force (Harrison 1993).

The internal structure of hybrid zones can be complex, often reflecting a patchy distribution of habitats and resources. Examples of "mosaic hybrid zones" have been documented in a variety of animals, and many plant hybrid zones seem to be of this type as well (Harrison and Rand 1989). There are also examples of broadly sympatric species that hybridize (occasionally or extensively) and yet remain distinct. The butterflies *Colias philodice* and *C. eurytheme* occur together throughout much of the United States, and a complete range of intermediates may be found at many localities (Hovanitz 1943). Nonetheless, the two species show no evidence of fusing. Ecological differentiation appears to play an important role in maintaining the distinctness of the parental types.

Presently, four core questions should be addressed around the hybrid-zone issue. The first question is about hybrid zone origins. Evolutionary biologists have debated this question since the late nineteenth century. Two contrasting scenarios have been proposed. One considers hybrid zones to be the results of secondary contact between populations that have differentiated in allopatry (Chapman 1892; Mayr 1942). Alternatively, hybrid zones may arise in situ in direction response to selection pressures (Endler 1977). Until now, considerable controversy still surrounds the question of hybrid zone origins and explanations for intergradation between distinct forms. The second one is of the dynamics of stable hybrid zone. Many hybrid zones appear to be relatively stable balance between dispersal and selection. There still need careful analysis of patterns of clinal variation, linkage disequilibrium, and introgression within and adjacent to hybrid zones to provide important insights into the strength of selection, dispersal rates, and genetic architecture of differences between the hybridizing taxa. The most interested question is the third one, which is upon hybrid zones fates. One possibility is that differentiated populations within the hybrid zones will fuse, yielding a single, possibly polymorphic species. Or, hybrid zones might result in the eventual extinction of one of the two hybridizing taxa, fusion and extinction are not mutually exclusive (Harrison 1990). Final question is for the causes and consequences of introgression. Hybridization could result in incorporation of alleles from one taxon into the gene pool of the other. The detailed patterns would be disclosed by the means of genetic analysis,

Genetic analysis of hybridization within hybrid zones

Hybrid zones are primarily of interest as natural laboratories in which genetic and ecological interactions between differentiated populations can be examined. Understanding

the causes and consequences of these interactions provides insights into a range of important problems in evolutionary biology and population genetics.

Hybridization and backcrossing to one or both of the parental types can result in incorporation of alleles from one taxon into the gene pool of the other. Anderson and Hubricht (1938) coined the term "introgressive hybridization" to describe this phenomenon. Attempts to identify and characterize patterns of introgression constitute an important component of the hybrid zone literature. Introgressive hybridization can lead to the production of recombinant genotypes that have properties different from those of either of parents. Anderson (1953) argued that introgression is an important source of new variation (more important than mutation) and that variants produced in this way are mostly likely to succeed in disturbed or changing environments. This issue has been debated for years but still remains unresolved (Harrison 1993).

Hybrid zones can be genetically described in many ways like linkage disequilibrium, covariance of quantitative traits, etc. Here we mainly concentrate on the clines within hybrid zone.

About the mechanism maintaining the cline in hybrid zone, there might simply be a balanced polymorphism, with an equilibrium that varies from place to place. Provided this equilibrium varies gradually enough, the shape of the cline directly reflects the local environment and has a shape that is independent of how far individuals move. For example, sickle cell anemia varies across Africa with the incidence of malaria. A special case of such "dispersal-independent" clines has been suggested by Moore (1977), who argued that hybrid zones might be maintained by selection favoring hybrids within a narrow region of intermediate habitat.

However, most hybrid zones cannot be explained in this way. First, dispersal is only negligible when clines are much wider than a characteristic scale, set by the ratio between the dispersal distance and the square root of the selection coefficient (Sliatkin, 1973). Second, if cline shape were determined directly by local selective conditions, one would expect it to vary considerably from place to place. In fact, clines often have similar width and shape across different transects. Finally, if clines at each locus or for each phenotypic trait were maintained in direct response to the environment, one would not expect them change in the same way or at the same place; in contrast, almost all hybrid zones consist of a cluster of parallel clines, often involving characters with no obvious functional relation (Barton and Hewitt 1989). Of course, there are exceptions to this argument, for example, *Theomomys bottae* in the Sangre de Cristo Mountains (Hafner *et al.* 1983). Their narrow width, consistent shape, and close concordance suggest that most hybrid zones are maintained by a balance selection and dispersal, the sharp disjunction that would be produced by selection alone is blurred by the random movement of individuals. Selection could act in many ways. The primary distinction is between adaptation to the external environ-

ment and selection against hybrids. The distinction is important, because it determines how the hybrid zone can move, or, how the sets of genes that distinguish the hybridizing populations compete with each other. If alleles are selected to fit their native habitat, the hybrid zone must lie at a particular point on an environmental gradient. If, on the other hand, selection acts against hybrids, the hybrid zone can move from place to place: it is then termed a "tension zone" (Key, 1968; Barton and Hewitt, 1985). In reality, different kinds of selection act in the same hybrid zone. Fortunately, the mechanism of selection has little effect on the shape of the clines; it is this fact that allows us to make inferences without needing to know just how selection is operating. Moreover, provided that selection is not too strong, cline shape does not depend on the local population structure: gene flow through both a continuous habitat and across a grid of demes or "stepping stones" can be approximated by diffusion (Nagylaki 1975). The effect of gene flow then depends on a single parameter defined as the standard deviation of the distance between parent and offspring, measured along a linear axis; it does not depend on the whole distribution of dispersal distances, which would be much harder to measure accurately.

Presently, cline is the central model to explain the gene flow within hybrid zone. During the past tens years, larger amount of molecular markers (isozymes, RAPD, SSR, etc.) have been used to empirical studies on clines of the hybrid zones. These studies have provided us deep insight for the process of macroevolution at a higher level.

Hybrid zone: evolution meets conservation

Issues upon species are always what both evolution and conservation care about. However, they hold different species concepts. Conservation biology usually utilizes the biological species concept (BSC), which defines a species as group of actually or potentially interbreeding organisms that are reproductively isolated from other such group. This concept of BSC, also called isolation concept, does not support the transient forms between two species or taxa, because it applies only one criterion that is reproductive isolation. Hybrid zones are not easily accommodated within this framework of BSC, and the entities that are joined by hybrid zones cannot simply be catalogued as either conspecific or as belonging to different species/taxa. In fact, the barriers that limit genetic exchange between hybridizing taxa are often semi-permeable (Key 1968; Harrison 1986), i.e., there is considerable variance in the extent to which alleles at different loci introgress. This observation has prompted the suggestion that species may need to be defined gene by gene (Barton and Hewitt 1981). For BSC, hybrid zones posed another serious problems for the recognition concept of species (Paterson 1985).

Whereas evolutionary biology adopts the phylogenetic species concept (PSC), which regards a species as the smallest diagnosable cluster of individual organism within

which there is a parental pattern of ancestry and descent (Cracraft 1983,1989; Nixon and Wheeler 1990). PSC does not rely on reproductive continuity (or discontinuity) as a necessary criterion for defining species and therefore has certain advantages.

Focusing on the hybrid zones, both conservation biology and evolutionary biology are seeking to answer the following questions as: what role of natural selection in species evolution is; what the exact function of genetic diversity is; and whether hybrid populations should be recognized as distinct Operational Taxonomic Units (subspecies or species), etc.. Particularly for conservation biology who now adopts the BSC, hybrid always is a hot potato, since hybridization definitely is a important way for gene exchange and conservative practices of endangered species, on other hand, present conservative theories are mainly based on the sterile concept of species, this makes hybridization subtle for explanations and conservative definition, whereas hybrid could be easy understood as a natural phenomenon to be explained in modern evolutionary biology. This holds up the progress of the conservation biology and its practices. It is very necessary to introduce hybrid-zone theory and a reasonable species concept into conservative practices, this would enhance endangered population conservation by better understanding gene exchange, moreover, it could offer us a broader and more open theoretical background to think about and treat with the conservative role of hybrids.

References

- Anderson, E. 1953. Introgressive hybridization [J]. *Biol. Rev.*, **28**: 280-307.
- Anderson, E. and Hubricht, L. 1938. Hybridization in *Tradescantia*. III. The evidence for introgressive hybridization [J]. *Am. J. Botany*, **25**: 396-402.
- Barton, N.H. and Hewitt, G.M. 1981. Hybrid zones and speciation [C]. In: W.R. Atriley and D.S. Woodruff. (eds) *Evolution and Speciation*. Cambridge:Cambridge University Press.
- Barton, N.H. and Hewitt, G.M. 1985. Analysis of hybrid zones [J]. *Annu. Rev. Ecol. Syst.*, **16**: 113-148.
- Barton, N.H. and Hewitt, G.M. 1989. Adaptation, speciation and hybrid zones [J]. *Nature*, **341**:497-503.
- Chapman, F.M. 1892. a preliminary study of the grackles of the sub-genus *Quiscalus* [J]. *Bull. Am. Mus. Natur. Hist.*, **4**: 1-19.
- Cracraft, J. 1983. Species concepts and speciation analysis [J]. *Curr. Ornithol.* **1**:159-187
- Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation [C]. In: D. Otte and J. Endler (eds) *Speciation and its consequences*. Sunderland, MA: Sinauer Association.
- Cracraft, J. 1997. Species concepts in systematics and conservation biology — an ornithological viewpoint [C]. In: M. F. Claridge, H. A. Dawah, and M. R. Wilson, (eds) *Species: the Units of Biodiversity*. Chapman and Hall, London.
- Cracraft, J. 2000. Species concepts in theoretical and applied biology: a systematic debate with consequences [C]. In: Q. Wheeler and R. Meier, (eds) *Species Concepts: a debate*. Columbia University Press, New York
- Darwin, C. 1872. *The origin of species*. 6th ed. London: John Murray.
- Endler, J.A. 1977. *Geographic variation, speciation, and clines* [M]. Princeton, NJ: Princeton University Press.
- Grant, V. 1981. *Plants speciation*. New York: Columbia University Press.
- Hafner, J.C., Hafner, D.J., Patton, J.L. *et al.*, 1983. Contact zones and the genetics of differentiation in the pocket gopher *Thomomys battae* [J]. *Syst. Zool.*, **32**: 1-20.
- Harrison, R.G. 1986. Pattern and process in a narrow hybrid zone [J]. *Heredity*, **56**: 337-349.
- Harrison, R.G. 1990. Hybrid zones: windows on evolutionary process [J]. *Oxford Surv. Ecol. Biol.*, **7**: 69-128.
- Harrison, R.G. 1993. *Hybrid zones and the evolutionary process*. New York: Oxford University Press.
- Harrison, R.G. and Rand, D.M. 1989. Mosaic hybrid zones and the nature of species boundaries [C]. In: D. Otte and J. Endler (eds) *Speciation and its consequences*. Sunderland, MA: Sinauer Association.
- Hewitt, G.M. 1988. Hybrid zones- natural laboratories for evolutionary studies [J]. *Tree*, **3**: 158-167.
- Hovanitz, W. 1943. Hybridization and seasonal segregation in two races of a butterfly occurring together in two localities [J]. *Biol. Bull.*, **85**: 44-51.
- Key, K.H.L. 1968. The concept of stasipatric speciation [J]. *Syst. Zool.*, **17**:14-22.
- Littlejohn, M.J. and Watson, G.F. 1985. Hybrid zones and homogamy in Australian frogs [J]. *Annu. Rev. Ecol. Syst.*, **16**: 85-112.
- Mayr, E. 1942. *Systematics and the origin of species* [M]. New York: Columbia University Press.
- Mayr, E. 1963. *Animal species and evolution* [M]. Cambridge: Belknap Press.
- Moore, W.S. 1977. An evaluation of narrow hybrid zones in vertebrates [J]. *Q. Rev. Biol.*, **52**: 263-277.
- Nagyaki, T. 1975. Conditions for the existence of clines [J]. *Genetics*, **80**:595-615.
- Nixon, K.C. and Wheeler, Q.D. 1990. An amplification of the phylogenetics species concept. [J]. *Cladistics*, **6**:211-223
- Petit, C., Bretagnolle, F. and Felber, F. 1999. Evolutionary consequence of diploid-polyploid hybrid zones in wild species [J]. *TREE*, **14**: 306-311.
- Rising, J.D. 1983. The Great Plains hybrid zones [J]. *Curr. Ornithol.*, **1**:131-157.
- Sliatkin, M. 1973. Gene flow and selection in a cline [J]. *Genetics*, **75**: 733-756.
- Stebbins, G.L. 1950. *Variation and evolution in plants* [M]. New York: Columbia University Press.
- Stebbins, G.L. 1959. The role of hybridization in evolution [J]. *Proc. Am. Philos. Soc.*, **103**: 231-251.
- Woodruff, D.S. 1973. Natural hybridization and hybrid zones [J]. *Syst. Zool.*, **22**:213-218
- Zirkle, C. 1932. Some forgotten records of hybridization and sex in plants [J]. *J. Hered.*, **23**: 433-448.
- Ziekle, C. 1934. More records of plant hybridization before koelreuter [J]. *J. Hered.*, **25**: 3-18.